THE CLASSIFICATION OF MALAYAN BAMBOOS

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IN STUDYING the bamboos of the Malay Peninsula, with the help of Gamble's great work (4), I found some difficulty in distinguishing between the genera *Gigantochloa* and *Oxytenanthera*, and I was struck by the resemblance in spikelet-structure between these genera and *Dendrocalamus*, though the latter is placed by Gamble in a different subtribe. This led to a consideration of the basis of Gamble's classification (little modified from the earlier one of Munro), namely fruit-structure, in which again I found agreement between *Gigantochloa* and *Dendrocalamus*; I also found that neither genus differed greatly from *Bambusa* in the gross structure of the fruit. A re-arrangement of Gamble's scheme therefore seemed necessary and was attempted. The result is given below, after discussion of the factors involved. It needs checking by examination of other species, and completing by examining the flowers of *Dinochloa* and the fruits of *Schizostachyum* and *Ochlandra*. I hope however that the scheme, though incomplete, will help others who may have the opportunity of examining bamboo flowers and fruits.

For the sake of convenience, I give here Gamble's conspectus of the subtribes of Indian bamboos:

1. ARUNDINARIEAE (none Malayan).
2. EUBAMBUSEAE. Stamens 6. Palea usually 2-keeled. Pericarp thin, adnate to the seed.
   Genera: *Bambusa, Thyrsostachys, Gigantochloa, Oxytenanthera.*
3. DENDROCALAMEAE. Stamens 6. Palea 2-keeled. Pericarp fleshy or crustaceous, separable from the seed.
   Genera: *Dendrocalamus, Melocalamus, Pseudostachyum, Teinostachyum, Cephalostachyum.*
4. MELOCANNEAE. Stamens 6 or more. Spikelets 1-flowered. Palea more or less similar to the flowering glumes. Pericarp crustaceous or fleshy, separable from the seed.
   Genera: *Dinochloa, Schizostachyum, Melocanna, Ochlandra.*

Fruits of Bambusa, Gigantochloa, and Dendrocalamus.

I found single almost ripe fruits on a plant of *Bambusa Tulda*, and on a *Gigantochloa*, which were flowering in the Botanic Gardens, Singapore, in 1945. These agreed together in essentials of structure, but did not agree with Gamble's statement for the Eubambuseae: "Pericarp thin, adnate to the seed." In both cases the apical part of the pericarp was thick and distinctly separate from the seed; the pericarp was much thinner toward the base of the fruit, but still easily separable from the seed, and the position of the embryo was not observable on the outside of the fruit. The

top of the fruit was abruptly narrowed to the style, the base only of which had become somewhat thickened. This structure agrees with that described by Gamble for *Dendrocalamus*, and with a fruit of *D. pendulus* Ridl. which I examined, except that the latter (as in some other species of *Dendrocalamus* described by Gamble) had the pericarp so thin near the base of the fruit that the position of the embryo could be seen. I therefore conclude that *Dendrocalamus* is not separable from *Bambusa* and *Gigantochloa* on fruit-characters.

The stamen-tube as a generic character.

Munro (10) and later authors have used the presence of a tube in place of free stamen-filaments as a character to distinguish genera, and Camus (3) even unites genera with stamen-tubes as a special subtribe. According to Gamble's generic diagnoses, a stamen-tube is present in *Gigantochloa* and *Oxytenanthera* and not in *Bambusa* and *Dendrocalamus*. But some species referred to *Oxytenanthera* have exactly the same spikelet-structure as those species of *Dendrocalamus* which have few florets; and two species included by Gamble in *Gigantochloa* (*G. heterostachya* and *G. latispiculata*) have in other respects the spikelet-structure of *Bambusa*. Further, united filaments occur in *Neohouzeaua* (Camus 3, Gamble 5), which in all other respects agrees with *Schizostachyum*, a genus which nobody considers related to *Gigantochloa*. It thus appears that united filaments have developed on at least three distinct evolutionary lines in the bamboos; therefore the character cannot be regarded as of basic importance in classification, and I doubt if it can be used to distinguish genera. I regard the subtribe Synandrae of Camus as a quite unnatural one.

Spikelet-structure in Bambusa, Gigantochloa, and Dendrocalamus.

It appears to me that the most significant feature of spikelet-structure in these genera is the development of the rachilla. In *Bambusa* the rachilla is elongate and jointed, with several internodes usually 2 mm. or more long, the lemmas of the fertile florets being all of about the same length. In the other genera the rachilla is very short, not jointed, the florets crowded closely upon it, the lower lemmas therefore shorter than the upper when several florets are present. On this basis it is easy to distinguish *Bambusa* on the one hand from *Gigantochloa, Oxytenanthera*, and *Dendrocalamus* on the other. A distinction on this basis involves the transfer of *Gigantochloa heterostachya* Munro and *G. latispiculata* Gamble to *Bambusa*, with which (as indeed Gamble realized) they agree in spikelet-structure, and I therefore propose the new binomials **Bambusa heterostachya** (Munro) comb. nov. (*Gigantochloa heterostachya* Munro in Trans. Linn. Soc. 26: 125. 1868) and **Bambusa latispiculata** (Gamble) comb. nov. (*Gigantochloa latispiculata* Gamble in Ann. Bot. Gard. Calcutta 7: 67. 1896).

We have now to distinguish between *Gigantochloa, Oxytenanthera*, and *Dendrocalamus*. Disregarding the stamen-tube (which is in fact sometimes

not at all easy to observe) and the fruit, we find that Gamble gives us very few other characters to use. Munro (10, p. 126) originally distinguished *Oxytenanthera* as having 1–3 florets, the palea (upper palea of Munro) of the uppermost or sole floret convex on the back, not keeled, the paleae of the lower florets (if present) 2-keeled; *Gigantochloa* had more florets, and the paleae all alike and 2-keeled. But Munro (and after him Gamble) included in *Oxytenanthera* the species *O. nigrociliata,* which had an imperfect uppermost floret described as unipaleate. The single organ present is called a palea by Gamble, but by its position I think it must truly be a lemma (lower palea of Munro); in any case it is quite unlike the true palea of the upper fertile floret in other species ascribed to *Oxytenanthera,* and is to me indistinguishable from the imperfect uppermost floret of species ascribed by Gamble to *Gigantochloa.* The two genera are in fact neither clearly distinguished nor clearly described by Gamble. As in *Oxytenanthera,* the palea of the uppermost perfect floret in *Dendrocalamus* is keelless, the paleae of the lower florets 2-keeled; Gamble states for some species that there may also be a small imperfect floret above the perfect ones.

I dissected spikelets of several species of *Gigantochloa* and *Dendrocalamus,* and of the Malayan species ascribed to *Oxytenanthera,* and found that Munro's distinguishing character, with slight emendation, is sufficient to separate *Gigantochloa* (including *Oxytenanthera nigrociliata* Munro) from the other two genera. In *Gigantochloa* there are always several fertile florets, all with 2-keeled paleae, and the spikelet is terminated by an imperfect floret consisting of a narrow lemma which is longer than all the other florets and usually projects slightly from the apex of a mature spikelet. In *Gigantochloa* also there is always (in my experience) a well-developed stamen-tube.

The distinction of *Oxytenanthera* from *Dendrocalamus* is not so easy. In both genera the uppermost fertile floret has an unkeeled palea, the lower florets (when present) have all 2-keeled paleae. In *Oxytenanthera* there are only 1–3 florets and there is no rudimentary terminal floret; in most species of *Dendrocalamus* there are more than 3 florets and there is sometimes a small rudimentary terminal floret. In *Oxytenanthera* there is a stamen-tube, in *Dendrocalamus* there is none. But what of *Dendrocalamus pendulus* Ridl. and a few allied species, which have one or two fertile florets, no rudimentary floret, and no stamen-tube? If we include these in *Dendrocalamus,* the distinction from *Oxytenanthera* on number of florets breaks down; if in *Oxytenanthera,* the distinction between the two genera rests only on number of florets, which is not satisfactory.

Vegetatively, all known species of *Oxytenanthera* (and *Dendrocalamus pendulus*) have relatively slender culms, often not strong enough to support their own weight, so that they rely on the support of neighbouring trees and may be described as semi-scandent. *Dendrocalamus,* on the other hand, has usually rather stout culms; but this does not apply to

D. strictus, and I doubt whether the character of slender as against stout culms could be used as a generic distinction. All things considered, I suggest merging *Oxytenanthera* with *Dendrocalamus*, pending further field study of the species.

The ovary of Schizostachyum.

Munro recognized that the ovary of *Schizostachyum* and other genera of his third group of bamboos was a peculiar structure. He wrote (10, p. 4): "The third division consists of berry-bearing Bamboos, in 8 genera. These are all extremely interesting from their peculiar fruit. The pistil generally appears to be contained in an envelope somewhat analogous to the sac, or utricle, or perigynium, which contains the seed of *Carex*. In the young state this is so closely attached to the style that it is almost impossible to separate it; in advancing to maturity it increases in various ways." Gamble was inconsistent in the terminology he used to describe this structure. Thus under *Teinostachyum Wightii* he wrote, "style included in the long beak of the perigynium," and under *T. Griffithii*, "ovary . . . narrowing into a long triquetrous beak forming the style."

I examined living flowers of *Schizostachyum brachycladum* (which flowers continuously in Singapore, but does not normally fruit), and dried flowers of other species, but saw no fruits. The ovary at flowering is slightly swollen, and is continued upward into a stiff angled style, with no sharp distinction between the two, and at the apex of the style are the short divergent stigmas. The style is hollow, with a free central strand of delicate tissue which is continuous below with the inner wall of the ovary, which surrounds the ovule. The annular hollow within the style is due to the breakdown of the thin-walled inner tissues, which do not keep pace in growth with the firm outer tissues. It is true that the stiff hollow style so formed is functionally somewhat similar to the utricle of *Carex*, though in homology and structure it is quite different. This peculiar style is the distinctive feature of all the later genera in Gamble's scheme. In *Dinochloa* the spikelets are very short, and the style also, but its structure appears to be the same; it has not however been well described, and I have seen no material.

Spikelet-structure of Schizostachyum.

In his work of 1896, Gamble does not appear to me to make a clear distinction between *Schizostachyum* and *Teinostachyum* (on p. 77 the spikelets of *Teinostachyum* are said to have one flower, on p. 97 many flowers); but in 1923 (5) he distinguishes the two by stating that *Teinostachyum* has several flowers in each spikelet, *Schizostachyum* only one. Now McClure has described a *Schizostachyum* with two florets in each spikelet (7); and I myself found that spikelets on plants of *S. brachycladum* growing in Singapore may have either one or two flowers. In such cases the palea of the lower floret is loosely convolute and usually distinctly 2-keeled toward the apex; that of the upper floret is tightly

convolute and hardly keeled. This not only does away with the distinction between *Schizostachyum* and *Teinostachyum*; it also breaks down their distinction from *Cephalostachyum*, which (according to Gamble's later paper) has a 2-keeled palea, whereas the others are said to have a palea convolute, not keeled. Indeed, Gamble himself was not consistent in this latter distinction, as in 1896 he described the palea of *Schizostachyum tenue* as 2-keeled. I suggest therefore that the genera *Schizostachyum*, *Cephalostachyum*, and *Teinostachyum* should be united; and probably *Pseudostachyum* should go with them.

The spikelets of *Schizostachyum* are articulate at the base of each floret, if there is more than one, as described by McClure (6, 8, 9), and the internodes of the rachilla are always long. Above the uppermost fertile floret the rachilla is extended to bear a more or less imperfect rudimentary terminal floret which is not jointed to it. In this character of articulation of the rachilla, *Schizostachyum* agrees with *Bambusa*, and I suggest that it is more likely to be related to *Bambusa* than to the *Dendrocalamus* group, with its very short unjointed rachilla.

Schizostachyum and Ochlandra.

The lodicules of *Schizostachyum* are relatively large, in the Malayan species usually 3 and sometimes more, often unequal in size, and there are sometimes intermediates between lodicules and stamens. I can see no sharp distinction on characters of lodicules and stamens between the one Malayan species included in *Ochlandra* by Gamble (*O. Ridleyi*) and those he places in *Schizostachyum*, and I would include *O. Ridleyi* in the latter genus; no fruits have been seen. The fruit of other species of *Ochlandra* may be distinctive, but it still lacks a proper description; and it is to be noted that McClure (8) has already united the small-fruited *Dinochloa* with the large-fruited *Melocalamus* (the two genera are placed in separate subtribes by Gamble), so size of fruit alone may not be a sufficient character on which to base generic separation. The only fruit of any of this group of genera which has been fully described is that of *Melocanna*, by Stapf (13).

Neohouzeaua, Dendrochloa, and Klemachloa.

These three genera, from Burma and Indo-China, appear to me redundant. *Neohouzeaua* Camus (2) admittedly differs from *Schizostachyum* only in the presence of a stamen-tube, and as above indicated I do not consider this a valid ground for generic distinction. I think that *Dendrochloa* Parker (11) also should be united to *Schizostachyum*; it has 5–7 florets in a spikelet, the paleae of the lower florets with 2 close keels, and the filaments of the stamens partially united (three together, two together, and one free). In spikelet-structure it shows no essential difference from the Malayan *Schizostachyum grande* Ridl. (of which I have examined type- and other material). *Klemachloa* Parkinson (12) is like *Dendrocalamus pendulus* Ridl. in spikelet-structure, having 1 or 2

florets, an unjointed rachilla, the uppermost or sole palea unkeeled, and free filaments; it has 2 or 3 lodicules, which are not found in *D. pendulus*, but are reported from a few species of *Dendrocalamus*. I would unite *Klemachloa* with *Oxytenanthera*, if that genus is maintained, or with a comprehensive *Dendrocalamus*.

Inter-relationships of bamboo genera.

Several authors have suggested that *Schizostachyum* and its allies, having (where present) large and sometimes numerous lodicules, in some cases quite large fruits and always a well-developed pericarp, and long rachilla-internodes, are the most primitive of existing bamboos. *Bambusa* agrees with these genera in its elongate rachilla-internodes, and in the almost universal presence of lodicules, but it differs in ovary-structure and in never having more than 3 lodicules, of which two are very fleshy like those of a great number of grasses. The short unjointed rachilla of *Dendrocalamus* and its allies seems likely to be derived from a primitive elongate state. In gross characters of ovary and fruit these genera do not differ appreciably from *Bambusa*, but more detailed study may indicate differences. I think it quite likely that *Bambusa* and *Dendrocalamus* represent distinct lines of advance from the primitive bamboo stock, from which *Schizostachyum* has changed less in inflorescence and floral structure.

A suggested re-classification.

Subtribe Melocanneae.

Ovary narrowed gradually into a stiff angled style which is hollow at flowering; fruit large or small, the pericarp free from the seed; spikelets 1- to many-flowered, the rachilla-internodes (if present) long, articulate; paleae of lower fertile florets (if present) more or less distinctly 2-keeled with keels close together; palea of uppermost (or sole) fertile floret tightly convolute; lodicules, if present, often large and flat, sometimes numerous.

Spikelets and style long (genera to be distinguished on fruit-characters?) *Schizostachyum*, *Ochlandra*, *Melocanna*.

Spikelets and style short ..... *Dinochloa*.

Subtribe Bambuseae.

Ovary abruptly narrowed to a slender style which is not hollow at flowering; fruit small, with pericarp free from seed; spikelets usually many-flowered, with distinct articulate rachilla-internodes; uppermost floret (or florets) usually imperfect; lemmas all about equal; lodicules usually 3, of which 2 are very fleshy and different from the third; stamen-tube rare.

Florets many; palea not bifid..... *Bambusa*.

Fertile florets 3; lowest palea deeply bifid..... *Thyrsostachys*.[1]

Subtribe Dendrocalameae.

Ovary and fruit as in Bambuseae; spikelets 1- to many-flowered, the rachilla very short, not articulate; lemmas in many-flowered spikelets very unequal, gradually longer toward apex of spikelets; uppermost floret perfect or imperfect, if perfect with an unkeeled palea, the other paleae 2-keeled; lodicules usually lacking, if present small; stamen-tube sometimes present.

All fertile florets with 2-keeled paleae; a terminal imperfect floret consisting of a long narrow lemma always present..... *Gigantochloa*.

[1] See N. L. Bor (1).

Uppermost or sole fertile floret with unkeeled palea, the paleae of remaining fertile florets 2-keeled; a terminal short imperfect floret present or not. *Dendrocalamus.*

(A possible distinction of *Oxytenanthera* from *Dendrocalamus* as follows: Fertile florets 1–3, with no imperfect terminal floret; stamen-tube often present ..... *Oxytenanthera.*

Fertile florets more than 3, with or without a short terminal rudimentary floret; stamens free..... *Dendrocalamus.*).

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